

How do Riverine Plumes of Different Sizes Influence Fish Larvae: do they Enhance Recruitment?

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Abstract. A review of the literature suggests that river discharge plumes strongly influence fish larvae and may play a significant role in the recruitment of local fishes. Some rivers drain large land masses to discharge shallow, turbid and nutrient-rich plumes that interact with ocean currents as well as with local oceanography and meteorology; these plumes may extend hundreds of kilometres offshore and alongshore. The frontal, or mixing, zone between plume and ocean waters is characterized by strong physical and biological processes. Physical dynamics, e.g. hydrodynamic convergence, and abundant nutrients (both river derived and upwelled) in the vicinity of discharge plumes often generate large stocks of phytoplankton, zooplankton and fish larvae, as well as high rates of primary and secondary production. Physical dynamics not only act to accumulate (and probably retain) biomass in frontal waters, but also transport organisms onshore, offshore and along the frontal boundary.

The mechanisms through which river plumes may influence recruitment are not clear. In considering the potential effects of scale of river discharge on recruitment, three alternative hypotheses are discussed. The short-food-chain hypothesis states that recruitment will be enhanced in the vicinity of river plumes because fish larvae experience superior feeding conditions, grow faster and thus experience a shorter stage duration and survive better. The total-larval-production hypothesis is that trophic conditions support such high total production of fish larvae that specific dynamics of growth and mortality are not relevant. The third hypothesis is that plumes facilitate the retention of fish larvae within a limited area, and it is the physical retention rather than production that explains the variation in recruitment. If one or a combination of these hypotheses explains the influence of river plumes on recruitment, then the greatest potential to affect fish recruitment may be possessed by large mid-latitude rivers carrying high suspended-sediment and nutrient loads that discharge into shelf waters to create well defined plumes where primary and secondary production are high.

Introduction

In all parts of the world where there are rivers, turbid low-density plumes extend into coastal waters, and the meeting of these waters is demarcated by a clear front (Largier 1993; Plate I). The size of plumes varies greatly, from those that are <10 km long (e.g. Botany Bay, Australia; Kingsford and Suthers 1994) to those that are over 100 km long (e.g. Amazon River, Brazil; Curtin 1986a, 1986b). The size of plumes varies according to size of the river, and 'pulse' and 'press' characteristics (*sensu* Bender *et al.* 1984) of the local rainfall, as well as snow melt, tidal regime, wind, topography of the entrance and the nature of ocean currents over the continental shelf (Le Fevre 1986; Dustan and Pinckney 1989; Uncles and Stephens 1990; Gelfenbaum and Stumpf 1993; O'Donnell 1993; Sharples and Simpson 1993).

Plumes and associated fronts cause major changes in physical oceanography and associated advective processes, changes in the distribution of plankton, and variation in the input of nutrients. A consequence of varying nutrient loads

is a potential cascade of changes in primary and secondary production (Le Fevre 1986). Processes in plumes are relevant to both pelagic and benthic fishes that are resident as larvae, juveniles and adults on continental shelves, and those that recruit to coastal environments (e.g. estuaries and reefs).

Hypotheses concerning the survivorship of fish during their early life history encompass all of the physical and biological factors that vary in plumes and fronts (Sinclair *et al.* 1986). The member/vagrant hypothesis of Sinclair (1988) has focused on the size and persistence of retention areas for variation in numbers of pelagic fish. Lobel and Robinson (1986) also argued that the retention of larvae in a tropical gyre was critical for the survival of reef fish to settlement. Other authors have argued that frontal convergence and other linear oceanographic features, including estuarine fronts, influence recruitment to coastal environments (Govoni *et al.* 1989; Kingsford 1990; Grimes and Finucane 1991). Abundant planktonic food is critical for the survival of ichthyoplankton, and variation in recruitment may track

temporal and spatial variability in the abundance of food (Cushing 1975; Lasker 1975). Abundant predators can have a great impact on mortality rates of cohorts of larvae (Moller 1984). Moreover, the vulnerability of larvae to predation will vary with nutritional condition (review Bailey and Houde 1989). In some circumstances mortality rates may still be high even when larvae are growing rapidly (Grimes and Finucane 1991; Lang *et al.* 1994).

Plumes have a major influence on waters of the continental shelf in many parts of the world, and these areas support most of the world's major fisheries. Therefore, plumes could potentially have a major effect on variation in numbers of fish that survive to recruitment (Sabatés and Maso 1990; Grimes and Finucane 1991). For example, historically low-density waters off the Nile delta supported a sardine fishery. This fishery collapsed with the building of the Aswan Dam in 1970, and a concomitant cessation of seasonal floods and nutrient input to coastal waters. Stocks have recovered to about one-third of their pre-dam levels after discharge rates from the dam were increased (Smetacek 1986).

The purpose of this paper is to review the evidence that plumes influence the magnitude of recruitment and to determine whether 'importance' correlates with the size of the plume and frontal region. First, we describe the physical and biological attributes of plumes that may influence fishes; second, we give an overview of how plumes and fronts affect the distribution of ichthyoplankton, physical transport and retention, feeding, growth and mortality rates. The concluding part of the review focuses on case histories that suggest that plumes and fronts have contributed to variation in recruitment, and considers the specific mechanisms that may influence recruitment variation.

Physical and Biological Attributes

Size and Types of Plumes and Associated Frontal Regions

The size of plumes varies greatly, from that generated by the Amazon River to small plumes that extend less than a kilometre from the mainland (Table 1). Plumes extend considerable distances from shore and often cover 50% or

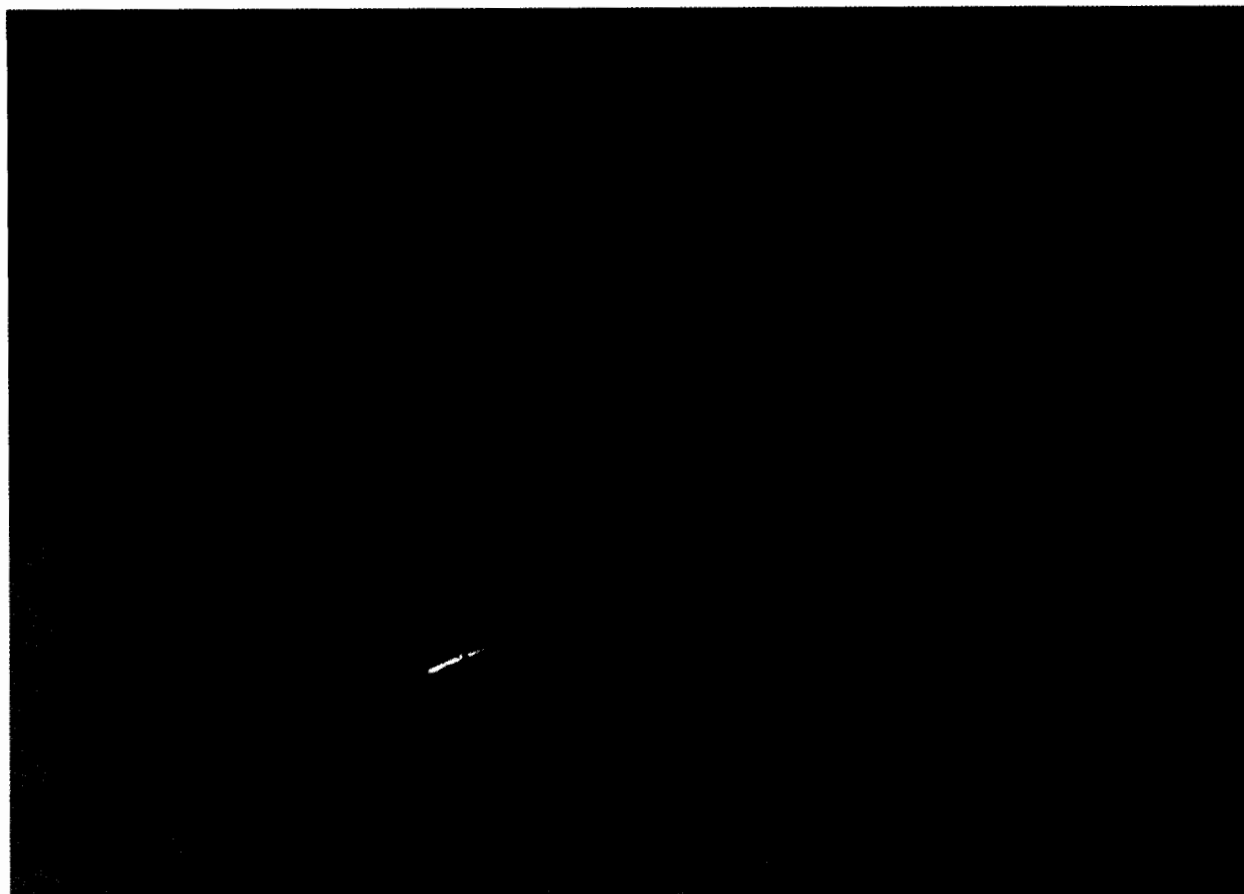


Plate I. Discharge of the Mississippi River into the Gulf of Mexico. The shallow turbid plume is disturbed by the action of the propeller of a tug boat crossing the turbidity front and exposing the underlying shelf water.

Table 1. Dimensions of various river discharge plumes

Distance from the mainland is calculated from the mouth of rivers or bays. Negative values refer to fronts positioned up rivers or in bays. A range is often presented because the position of plume fronts can vary with time. Plume sizes: S, small (<20 km from shore and flow <100 m³ s⁻¹); M, medium (21–50 km and 101–5000 m³ s⁻¹); and L, large (>50 km and 5000 m³ s⁻¹). Where plumes are generated in sounds between the mainland and islands, width of the shelf is not given. Most details are from sources but some distances were estimated from maps where data were not available

Country	River/Bay	Size	Distance of front from mainland (km)	Distance along the coast (km)	Width of the mouth (km)	Flow of water (m ³ s ⁻¹)	Depth of plume within 10 km of front (m)	Zone in which the front is located (km)	Width of shelf (km)	Source
Brazil	Amazon	L	120–200	500	400	200000	1–10	80–100	200–300	Curtin 1986a
USA	Mississippi	L	<100	<800		18300	10–12	2–20	50	Gunter 1979
Canada	Fraser	M	30–40	<100	20–30	1000–8000	ND	≈10	Sound	Mackas and Louttit 1988
Spain	Ebro	M	50	≈90	<1	ND	10–15	ND	45	Sabatés 1990
USA	Connecticut	M	10	60	5	560	1	ND	Sound	Garvine and Monk 1974; Garvine 1986
France	Rhone	M	≈8	≈100	≈1	500–5000	ND	2–3	50	Leveau <i>et al.</i> 1990; Sabatés 1990; Sournia <i>et al.</i> 1990
USA	Chesapeake Bay	M	50–130	165	20	ND	ND	ND	65–120	Garvine 1986; Boicourt 1973
Australia	Botany Bay, Cooks, Georges	S	–2–10	2–10	1	ND	1–4	14	25–50	Kingsford and Suthers 1994
Wales	Seiont	S	–0.3–0.3	ND	0.8	5	0.3–1	0.6	ND	Simpson and Nunes 1981
Australia	Burdett	S	30	ND	0.8	≈0.2	ND	5	100–120	Thorold and McKinnon 1992
Zaire	Zaire (Congo)	L	111–185	741	11	45000	ND	ND	80	Eisma and Van Bennekom 1978

more of the continental shelf. For example, the Amazon River plume extends up to 200 km over a shelf that is 200–300 km wide (Curtin 1986a, 1986b). The small plume from Botany Bay, Australia, has been measured at distances of 11 km from the mainland (Kingsford and Suthers 1994), and this is over a shelf that measures 25–30 km wide. Freshwater discharge and its associated sediment load influences the shape of the shelf. For example, off the Amazon River it manifests itself as a conspicuous topographic 'cone' that is recognizable to depths of 2000 m and 400 km from land (Curtin and Legeckis 1986). Strong physical and visual signals of plumes can be observed at great distances along the coast, as well as across the shelf. The Amazon River plume can still be measured up to 500 km, the Mississippi 200 km, the Rhone 150–200 km and the Connecticut 60 km alongshore from the mouth. The magnitude of transport alongshore will vary greatly with the direction and intensity of ocean currents (e.g. Gelfenbaum and Stumpf 1993; Kingsford and Suthers 1994). Thus, single rivers may influence tens to hundreds of square kilometres of shelf waters. In pulse events, such as cyclone-associated rain, the plumes of multiple rivers can merge over the shelf to form a single turbidity front. For example, in 1990 Kingsford and Suthers (unpublished) flew along 50 km of the coast of New South Wales, Australia, after a major pulse event. Individual plumes associated with Botany Bay (Georges and Cooks Rivers), Port Jackson (Parramatta River) and the Hawkesbury River had coalesced to form a turbidity zone that extended 20–30 km into clear oceanic waters. Multiple rivers contributing to a low-density anomaly are also found in many other parts of the world (e.g. Japan, Yanagi and Takahashi 1988; Spain, Sabatés and Maso 1990; Wales, Sharples and Simpson 1993; USA, Gelfenbaum and Stumpf 1993). Therefore, plumes of different sizes are sometimes nested within a large oceanographic feature. For example, fresh water from nine rivers in the South Atlantic Bight of the USA forms a nearshore low-salinity region with a front that can extend 20–30 km from shore. In some conditions, southward-flowing low-salinity water can be detected as far south as Florida, where there is no known local source of fresh water (Blanton and Atkinson 1983). The dimensions of plumes increase rapidly in flood conditions and the turbidity signal is much stronger. In May 1993, flow of the flooding Mississippi River was $42000 \text{ m}^3 \text{ s}^{-1}$, over double the average flow of $18300 \text{ m}^3 \text{ s}^{-1}$. Similarly, the average daily discharge from Mobile Bay is $1850 \text{ m}^3 \text{ s}^{-1}$, but in peak flood this can reach $15000 \text{ m}^3 \text{ s}^{-1}$ (Gelfenbaum and Stumpf 1993).

The size and shape of plumes and their associated fronts is variable, and will depend primarily upon the nature of the tidally induced turbulent mixing, the dimensions and shape of the estuary and adjacent shelf area, and the rate of

freshwater discharge (Bowman 1988). If the lower river valley is narrow and constricted and falls steeply to the sea, and if the river discharge is large, then the plume will consist mainly of fresh water and most mixing will occur offshore. For example, the second-largest river (in terms of flow) in the world, the Zaïre (Congo), drains the large central-African basin and falls about 500–600 m before it reaches the coast and flows across the continental shelf via a submarine canyon. Thus, the leading edge of the plume is 700 km offshore and the plume is relatively narrow. If, as in the case of the Chesapeake Bay, the lower river basin is wide and gently sloping and the river flow is relatively weak, then there is appreciable infusion of seawater into the river valley; the lower river has estuarine characteristics and a well developed plume is not present (Boicourt 1973). The lower Amazon River basin is wide, but the flow is the highest in the world and the river encounters a shallow sill before it reaches the shelf, thereby creating a well developed plume detectable 200 km offshore. Ocean currents deform plumes and facilitate alongshore transport of low-density water (e.g. Curtin 1986b). In some cases currents reverse so that alongshore transport reverses direction through time (e.g. Garvine 1974; Kingsford and Suthers 1994). Wind can force plumes in a landward direction or alongshore. For example, Gelfenbaum and Stumpf (1993) found that wind forced a plume from Mobile Bay in the northern Gulf of Mexico close to the shore. Although the bay discharged $7000 \text{ m}^3 \text{ s}^{-1}$, the plume extended only 1.6 km from the shore, and there was considerable transport ($>10 \text{ km}$) alongshore.

Where rivers discharge into the sea, creating a freshwater or low-salinity plume, the water column has a characteristic hydrographic structure caused by the abutment of two water masses with distinctly different densities (e.g. Fig. 1). The lighter plume water will tend to flow over the heavy ocean water, until the horizontal pressure gradient is balanced creating an approximate geostrophic balance (Bowman and Iverson 1978). The pycnocline will slope downward from the surface, away from the denser water mass, and always toward the coast in the case of river discharge (Franks 1992). A broad mixing zone between plume and ocean water where isohalines are closely spaced and approach the surface represents the frontal zone (e.g. Fig. 1). The width of the frontal zone is strongly influenced by the wind, which may increase or decrease it (Csanady 1978; Hseuh and Cushman-Roisin 1983; Ou 1984). The frontal zone will often have a curved S-shape in vertical cross section due to the flow of less-dense water over the deeper denser water (Franks 1992). Often the lateral boundaries of the buoyant plume are extremely sharp features (Garvine and Monk 1974). Turbidity fronts, the seaward projection of concentrated suspended particulate matter, represented by sharp colour discontinuities, are often nested within the frontal zone (Garvine and Monk 1974).

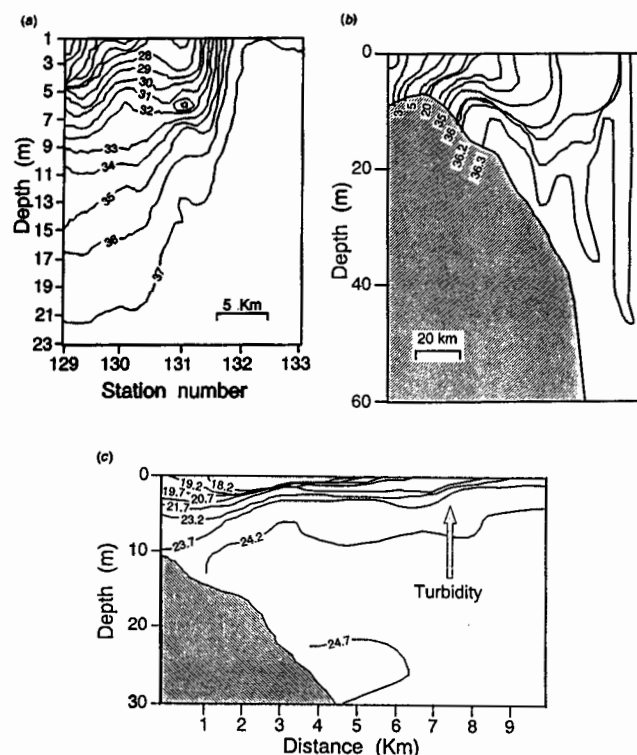


Fig. 1. Salinity profiles along transects of (a) the Mississippi and (b) the Amazon River; (c) density profile of the Botany Bay plume, Australia.

Plumes of all sizes may generate strong density gradients, where low-density plumes flow over higher-density coastal waters (Garvine 1986; Yanagi 1987; Sournu *et al.* 1990). Plumes from great rivers, such as the Amazon (18% of the world's fresh water, Curtin 1986a), always have a strong density gradient that characterizes the plume because there is always high freshwater discharge. Water density is a combination of variation in salinity and temperature. Hence, in some cases the low-density layer can originate from the solar heating of seawater on its tidal transit in a shallow estuary. This is particularly true of plumes that are influenced by rivers that do not have great drainage basins, e.g. the Rivière d'Etel on the south coast of Brittany, France, where no influence of salinity has been detected (Le Fevre *et al.* 1981; Le Fevre 1986). Kingsford and Suthers (1996) describe similar conspicuous low-density plumes of turbid water in Botany Bay, Australia, where only slight differences in salinity between oceanic and plume waters were detected. With adequate information on salinity, salinity contribution to density, river discharge, thermal expansion of water, net heat flux per unit area and specific heat, the contribution of surface heating and freshwater discharge can be calculated (Yanagi and Takahashi 1988).

Frontal zones and their embedded turbidity fronts have different temporal and spatial scales. Frontal zones of large

ivers are more or less permanent and may have a spatial scale of kilometres; for example, this zone is 25 km wide in the Amazon River plume (Curtin 1986a) and 6–8 km wide in the Mississippi River plume (Grimes and Finucane 1991), or as small as 20 m wide in the smaller Connecticut River plume (Garvine and Monk 1974). Turbidity fronts are ephemeral with a time scale of hours, generating and dissipating within a tidal period (Bowman 1988; Govoni and Grimes 1992). For example, turbidity fronts lasted 3–4 h, developed and dissipated in 15–30 min and had a spatial scale of 5–100 m in the large Mississippi River plume (Grimes and Finucane 1991); the spatial scale of the turbidity front in the small Connecticut River plume was 0.5 m (Garvine and Monk 1974). Turbidity fronts intensify during ebbing tides when seaward surface slopes are greatest (Bowman 1988; Grimes and Finucane 1991). Although frontal features may be only a few metres wide, they may be tens or even hundreds of kilometres long, depending on the size and shape of the plume. Such linear oceanographic features do not fit well into conventional categories of spatial scale (Kingsford 1990).

Plumes are shallow features, typically of the order of a few metres (Table 1). Even in large rivers like the Amazon and Zaïre (Congo), the depth of the low-salinity plume varies between 1 and 15 m during periods of minimum and maximum flow (Curtin 1986a; Eisma and Van Bennekom 1978). Thus, frontal circulation tends to be restricted to surface waters, with the dynamics controlled by surface pressure gradients, interfacial friction and entrainment across the frontal interface.

Surface water converges at plume fronts primarily owing to strong horizontal density gradients and the resulting pressure gradients that are produced within and below sloping isopycnals of the frontal layer (Garvine and Monk 1974). The cross-frontal circulation is characterized by vigorous convergence on both sides of the front, typically higher on the high-density (seawater) side than on the low-density (plume water) side, e.g. an average of 0.5 and 0.2 m s⁻¹, respectively in the Connecticut River plume (Garvine and Monk 1974) and 0.2 and 0.1 m s⁻¹ for the Mississippi River plume (Govoni and Grimes 1992). The horizontal motion of the high-density water apparently continues unabated to the bottom (Garvine and Monk 1974). As surface waters converge, planktonic organisms move passively with the water toward the front where converging water masses move downward owing to gravity. Surface-seeking and buoyant organisms accumulate at the surface as they resist downward movement. This is a local, but important, transport mechanism that can concentrate larval fish and zooplankton and account for the high densities of these in plume fronts. For example, Govoni and Grimes (1992) measured surface convergence velocity in the Mississippi River up to 0.8 m s⁻¹ and found that the

observed velocity was always greater than the velocity calculated from the density gradient alone; they concluded that the observed velocity was the sum of the density-driven velocity plus the tidally driven velocity inherent in shelf waters. They used an advection–diffusion model (Olson and Backus 1985) to simulate surface densities of larval fish at the front that agreed well with observed values. Convergent velocity of surface waters, and perhaps also the concentrating effect on plankton, do not appear to be dependent on the scale of the river plume. Largely overlapping surface convergence velocities (up to 0.8 and 0.7 m s⁻¹, respectively) have been measured for the large Mississippi River and the small Connecticut River plumes (Garvine 1977; Govoni and Grimes 1992).

Primary and Secondary Production

Riverine discharge plumes are generally among the most productive places in the sea, and this seems so for both primary and secondary production. Phytoplankton biomass (chlorophyll) and primary production, as well as zooplankton biomass and concentration are all conspicuously elevated near riverine plumes (Table 2). The Zaïre (Congo) River discharge plume off central Africa may be an exception, in that phytoplankton biomass and primary production associated with the plume are hardly above values reached in the Atlantic Ocean outside the plume (Cadee 1978). The narrowness of the Zaïre River plume leads to a very short flushing time of brackish water. The short residence time limits the opportunity for phytoplankton to use nutrients advected with river water, and thus phytoplankton biomass and primary production are very low (Eisma and Van Bennekom 1978; Cadee 1978). High production may be driven principally by land-derived nutrient concentrations associated with the river discharge (Riley 1937; Lohrenz *et al.* 1990). Grange and Allanson (1995) compared two estuaries in South Africa with contrasting freshwater inflows and concluded that, as a result of high sustained freshwater inflow, the concentration of seston (total suspended organic matter) was an order of magnitude higher in the high-flow estuary. However, Demaster and Pope (1996) reported that despite the large influx of nutrients from the Amazon River and upwelled sources, the largest supply of nutrients to phytoplankton on the outer shelf comes from internally regenerated biogenic material. Several additional authors have suggested that nutrient enrichment of plume waters and high production were associated to some degree with upwelling, for example in the Columbia River plume (Conomos *et al.* 1972), the Fraser River plume in the Strait of Georgia (Harrison *et al.* 1991) and the Amazon River plume (Demaster and Pope 1996).

The highest values for primary and secondary production associated with plumes occur at intermediate salinities, i.e.

at the frontal region where the most active mixing of low-salinity plume water and high-salinity seawater occurs (Table 2; Figs 2 and 3). This pattern of production along salinity gradients seems to be controlled mainly by the interaction of light and nutrients, i.e. due to the mixing of nutrient-rich but turbid plume waters (where photosynthesis is primarily light limited) with clear but nutrient-poor seawater (where photosynthesis is mainly nutrient limited) (Riley 1937; Ryther and Dunstan 1971; Bruno *et al.* 1980; Skylar and Turner 1981; Boynton *et al.* 1982; Lohrenz *et al.* 1990; Smith and Demaster 1996). The pattern of production in a plume will also vary with the amount of nutrient input from the surrounding land mass and the river basin, and with flow characteristics that determine whether nutrients are stripped from riverine waters prior to reaching the sea. Conomos *et al.* (1972), Harrison *et al.* (1991) Franks (1992) and Demaster and Pope (1996) have implicated nutrient enrichment of surface waters by entrainment of deeper waters along the frontal zone between opposing plume and ocean waters. Franks (1992) suggests that diffusive mixing of nutrient-rich plume water is the main mechanism promoting phytoplankton production at fronts, but upwelled water may be an additional source of nutrients supporting

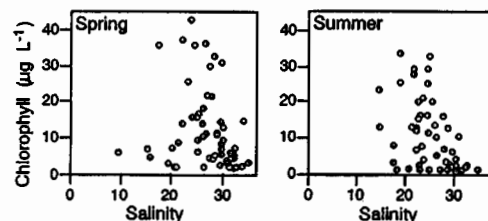


Fig. 2. Distribution of chlorophyll along salinity gradients associated with the Mississippi River discharge plume (redrawn from Dortch and Whittedge 1992).

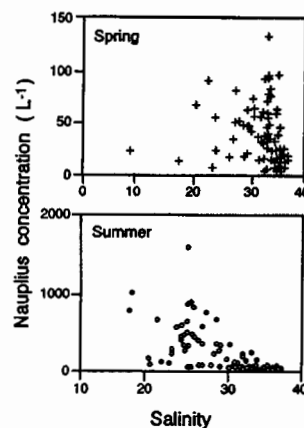


Fig. 3. Distribution of copepod nauplius concentration along salinity gradients associated with the Mississippi River discharge plume (redrawn from Dagg and Whittedge 1990).

phytoplankton growth. Two-celled circulation causes convergence to the front and downwelling along the pycnocline. Upwelled water converges to the front and may supply phytoplankton at the front and within the pycnocline with nutrients otherwise unavailable to them.

High primary productivity and phytoplankton biomass at intermediate salinities also apparently support high secondary production through zooplankton grazing (Dagg and Whitledge 1991; St John *et al.* 1992). Govoni and Grimes (1992) demonstrated the role of hydrodynamic convergence interacting with buoyancy and behaviour in explaining the surface accumulation of larval fish at the Mississippi River plume front; presumably this physical mechanism would also influence the spatial distribution of some zooplankton.

Although data available on production associated with river plumes of differing scales are rather limited, they suggest that accentuated production is scale dependent, i.e. enhanced production increases with the size of the discharge plume (Table 2). For example, the effect for large rivers like the Mississippi and Columbia off eastern and western North America and the Changjiang (Yantze) off China is pronounced, whereas production at small and medium-sized river discharges like the Rhone off western Europe, the Ashley and Cooper off eastern North America and the Burdekin off eastern Australia (McKinnon and Thorrold 1993) is less accentuated. However, Franks (1992) states that enhanced primary production at fronts is uncorrelated with the theoretical or actual scale of the front itself, probably because the processes generating the production are uncorrelated with the scale of the front, i.e. primary production and transfer to higher trophic levels may be scaled by nutrient inputs rather than river size following a Redfield approach as outlined in Harris (1986).

Other factors such as latitude, season, and the physiography of the continental shelf also seem to influence the pattern of production associated with plumes. Both phytoplankton biomass and primary production are generally higher and more accentuated at intermediate salinities in mid-latitude river discharges such as the Mississippi, Changjiang (Yantze) and Columbia than for low-latitude rivers such as the Zaire (Congo) and Amazon (Cadee 1975). Perhaps the production signal associated with tropical river discharges is lower because the discharge of low-density plume waters into already strongly thermally stratified low-latitude (tropical) shelf waters intensifies stratification and retards entrainment of nutrient-rich waters below the plume (Ryther and Dunstan 1971). Additionally, year-round high temperatures in the tropics may promote the stripping of nutrients from river waters before they reach the sea. The natural relationships between river and plume characteristics and production may be at least partly obscured by large anthropogenic nutrient enrichment of

some rivers like the Mississippi (e.g. see Turner and Rabalais 1991).

In spring, phytoplankton biomass in the Mississippi River discharge is somewhat higher than in summer (Fig. 2), whereas copepod nauplius concentration is much higher in summer than in spring (Fig. 3). For both of these properties, highest levels occurred at slightly higher salinities in spring than in summer (Figs. 2 and 3), perhaps because increased turbidity and plume size associated with spring flood waters causes the region of light-limited primary production to move further offshore and occur at higher salinities. St John *et al.* (1993) used a physical-biological numerical model to understand the effects of the Fraser River plume on primary production. During spring, fresh water stabilized the surface layer resulting in a shallow depth of mixing for phytoplankton, thus increasing light available for photosynthesis and promoting early onset of the spring phytoplankton bloom in the discharge area. During summer, the increased buoyancy from the river plume suppresses wind mixing of nutrients into the euphotic zone because more energy is required to break down increased stratification, and thus it reduces primary production in the vicinity of the Fraser River discharge.

There are differences in primary production associated with coastal/continental shelf physiography (Fig. 4). Where rivers discharge onto open shelves (or into a submarine canyon in the case of the Zaire River), highest production is associated with intermediate salinities (20–30). In contrast, the Amazon River discharge encounters a shallow sill deposited near the river mouth by its enormous sediment load; this results in intense vertical mixing of plume and shelf waters. Consequently, turbid plume waters do not extend far out onto the continental shelf, and highest primary production occurs at relatively low salinity (≈ 10) (Cadee 1975; Edmond *et al.* 1981).

Plumes and Fish

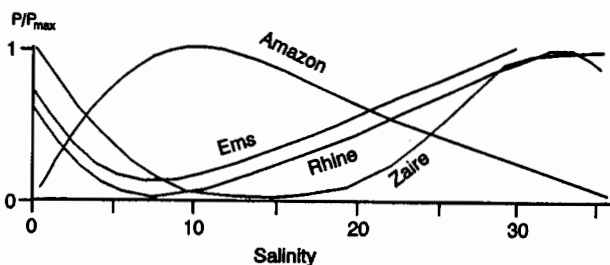


Fig. 4. Relative primary production *in situ* plotted on salinity for the tropical rivers Amazon and Zaire (Congo) compared with summer production in the temperate rivers Rhine and Ems (redrawn from Cadee 1975).

Distribution of Fish

Although there are data on zooplankton in plumes and adjacent open water (reviewed in Le Fevre 1986) and an extensive literature on fish larvae in estuaries (e.g. Rijnsdorp *et al.* 1985), there are surprisingly few data on the distribution of ichthyoplankton where sampling has been stratified according to oceanographic features (e.g. plume, front and ocean).

We have identified three different types of studies that are relevant to the distribution of fish in and around plumes: (1) sampling that was done tens to hundreds of metres each side of fronts; (2) sampling in and out of broad frontal regions (kilometres to tens of kilometres) and (3) sampling done in a grid pattern over a broad spatial scale, with the abundance patterns of fish superimposed on oceanographic density or salinity contours.

In general, fish larvae are more abundant in the vicinity of river discharge plumes. For example, average densities of larval fish around the Mississippi River discharge (Ditty 1986; Govoni *et al.* 1989; Grimes and Finucane 1991) are up to 20× higher than densities reported along Loop Current fronts in the open Gulf of Mexico (Richards *et al.* 1989). It is also clear that above-average concentrations of ichthyoplankton are often found in the fronts of plumes (Table 3). A primary mechanism contributing to the concentrating effect is hydrodynamic convergence (Govoni and Grimes 1992), although the active mechanism of spawning by adults in the most productive waters is also possible (Sabatés and Maso 1990). Highest concentrations are not always found in the front, and this may relate to

variation in physical convergence, which can change according to the state of the tide (Dustan and Pinckney 1989; Grimes and Finucane 1991; Govoni and Grimes 1992), and to interactions with ocean currents, wind shear, freshwater input, topography, differences in water density, the behaviour of ichthyoplankton and the availability of planktonic food (O'Donnell 1993; Kingsford and Suthers 1996). It is also possible that patterns of convergence facilitate the concentration of small fish, but that when the physical convergence dissipates there is still a patch of plankton of a broad size range. The patch may maintain its integrity (from minutes to hours) before it disperses (Kingsford and Suthers 1996). As a result, a great deal of patchiness would be expected in the broad frontal region and this is often found (Govoni and Grimes 1992). Densities of fish in fronts are up to 18×, and fish eggs up to 33×, more concentrated than in surrounding waters (i.e. plume and ocean, Table 3). Many studies on fishes associated with fronts entailed sampling at the surface during the day, and because fish and other plankton commonly migrate to the surface at night a different assemblage of fishes may be affected at this time. Also, this temporal variation in abundance at the surface, as well as their contagious spatial distribution, will contribute to the perceived concentrations of fish larvae as well as their contagion.

It is likely that the broad km-scale frontal region is relevant to the biology of fish larvae since it is within this entire region that they are concentrated (Grimes and Finucane 1991). The size of frontal regions can be substantial for both small and large plumes (Table 1), and

Table 3. Magnitude of aggregation of fish larvae and eggs in waters of plume (P), front (F) and ocean (O)

Scale: Large=area traversed by the plume; Small=near and in actual front. Type: Developmental phase of fish. Concentration: F/P and F/O indicate range of the magnitude of concentration. Equipment: mesh of the net (mm) and the device used; tow=towed net, seine=plankton-mesh purse-seine. *m*, number of mean values

Scale	Type	Water Mass			Unit	Concentration		<i>m</i>	Equipment	Source
		P	F	O		F/P	F/O			
Large (kms)	larvae	110–150	110–180	110–150	1000m ⁻³	1–1.2	1–1.2	2(day)	0.5 tow	Govoni and Grimes 1992
Large (kms)	larvae	110–240	390–540	110–240	1000m ⁻³	1.6–5	1.6–5	2(night)	0.5 tow	Govoni and Grimes 1992
Small ^A	larvae	50–100	1000–2600	50–100	1000m ⁻³	10–52	10–52	3(day)	0.5 tow	Govoni <i>et al.</i> 1989
Small (<200 m)	eggs	6–30	4–75	2–19	m ⁻³	0.25–9	2.5–18	6(day)	0.28 seine	Kingsford and Suthers 1994
Small (<200 m)	larvae	19–140	2–320	8–12	45m ⁻³	0.05–	0.3–16	6(day)	0.28 seine	Kingsford and Suthers 1994
Small (<200 m)	larvae	1–49	5–36	1–16	40m ⁻³	–9.4–14.5	–2–6.3	12(day)	0.5 tow	Kingsford and Suthers In press
Small ^B	larvae eggs	40–100	700–1350	40–100	100m ⁻³	7–33	7–33	1(day)	0.38 tow	Sakamoto and Tanaka 1986

^ATens to hundreds of metres. ^BHundreds of metres.

temporal variation in the size of plumes and associated frontal regions may cause significant biological variation in numbers of fish influenced by conditions in the plume. Some taxa appear to be characteristic of waters of the plume and front. These species may be good candidates for the studies of links between variation in recruitment and the biological and physical attributes of frontal regions and the properties of plumes. Concentrations of ichthyoplankton associated with river plumes, and their frontal regions in particular, is of intense interest for understanding the population dynamics of affected species. How does high primary and secondary production and physical oceanography in these regions influence associated fish larvae and small juveniles?

Transport and Retention

The physical oceanography of plumes may facilitate one or a combination of the following: (1) transport offshore in the plume and transport onshore in sub-plume waters; (2) transport of fish along fronts to potential settlement sites; (3) retention of fish in the vicinity of the plume and frontal region; (4) retention of prey and predators in the vicinity of the plume and frontal region (Fig. 5). It seems likely that the physical mechanisms of retention and transport, the size of plumes and the concentrations of other zooplankton (predators and prey; see *Feeding, Growth and Mortality* section below) will influence the survivorship of fish to recruitment.

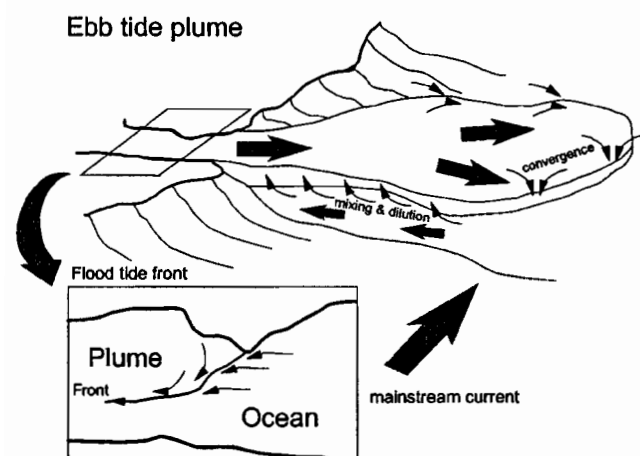


Fig. 5. Diagrammatic presentation of the physical oceanography of plumes and associated circulations at the front and beneath the plume. Mixing and dilution occurs on the underside of the plume as oceanic waters are advected into it. Convergence occurs along the edges, and waters are subducted toward the subsurface pycnocline. Flood-tide fronts are often generated at the entrance to estuaries and can be strongly influenced by topography.

It is well known that current direction varies with depth in the vicinity of estuaries (Fig. 5) and that oceanography combined with larval behaviour can facilitate retention (Table 4). For example, in the plume of the Connecticut River there is movement of water toward the frontal margin in the upper 1–2 m, while at greater depths there is transport onshore and away from the front (Garvine and Monk 1974; Garvine 1986). This is generally a result of surface water being entrained into the plume and coastal waters flowing in to replace it (Fig. 5). The intensity of these patterns of flow can be increased by the action of the wind. The offshore movement of surface waters can be accelerated if Eckman transport is offshore (Blanton and Atkinson 1983). During intense storms, wind-induced inflow can occur in surface waters (Goodrich *et al.* 1989).

Fish and invertebrate larvae may behave in such a way that early stages are advected in one direction (e.g. offshore) and larger larvae are advected in the other (e.g. onshore, Epifanio 1988). Research has tended to focus on tidal currents rather than plumes per se (e.g. Rijnsdorp *et al.* 1985). Larval smelt were retained in the well mixed part of the St Lawrence estuary by migrating to the surface during flood tides and to the bottom during ebb tides so as to minimize net downstream displacement (Laprise and Dodson 1990). In contrast, tomcod, *Microgadus tomcod*, remained deep in the water column, and their accumulation at the head of the estuary appeared to be the result of upstream transport by net residual circulation rather than active tidal migrations. Both of these behaviours combined with physical dynamics resulted in retention, therefore different behavioural responses can result in retention. Sinclair (1988) argued that all small fish behave in a way that allows them to maintain position and lower the chances of export from retention areas via advection. Laprise and Dodson (1990) pointed out that changes in behaviour may occur for various reasons such as a change in the buoyancy of fish as swim bladders develop or disappear. Regardless of the reasons for changes in the behaviour of fish, a combination of behaviour and physical dynamics can facilitate transport and retention.

Investigations on the direction and magnitude of transport and retention of larval fish and invertebrates has a strong emphasis on vertical processes. However, there are strong advective processes associated with the fronts themselves that can influence retention in the vicinity of plumes and transport along them (Table 4). For example, fishes associated with plumes can be transported a considerable distance along (e.g. upstream) 'axial fronts' that form on flood tide in estuaries and rivers with a strong tidal influence (Nunes and Simpson 1985; Brown *et al.* 1991). Kingsford and Suthers (1994) described the jetting of particles along fronts in Botany Bay, Australia, that could result in transport of larvae to particular sites in coastal

Table 4. Influence of some plumes and fronts on transport and retention of zooplankton

ND, no data. Retention: the oceanography of the plume has a physical role, or potential one, in retaining zooplankton. Transport: has a physical role in transporting zooplankton offshore or onshore; state of the tide is indicated if specified

Scale	Type of plankton	Retention		Transport			Source
		Plume	Front	Plume	Below Plume	Front	
kms	ND	Potentially	Along	Offshore	Onshore	Along	Garvine and Monk 1974; Garvine 1986
kms ^A	ND	ND	ND	ND	ND	Axial front, along (flood)	Brown <i>et al.</i> 1991
kms	ND	ND	ND	Onshore	ND	Offshore some along (ebb)	Sarabun 1993
kms	ND	ND	ND	ND	ND	Axial front, along (flood)	Nunes and Simpson 1985
kms	ND	ND	ND	ND	ND	Offshore (ebb)	Sharples and Simpson 1993
kms ^A	bivalve larvae	ND	Eddy and front	ND	ND	ND	Mann 1988
kms	fish	ND	Along (flood and ebb)	Offshore (ebb)	ND	ND	Kingsford and Suthers 1994
kms	ND	ND	ND	Offshore plus wind interaction	Onshore	ND	Blanton and Atkinson 1983
kms	fish and zooplankton	ND	Along (flood and ebb)	ND	ND	ND	Grimes and Finucane 1991
kms	fish	ND	Along (flood and ebb)	ND	ND	ND	Govoni and Grimes 1992

^AData from inside the mouth of an estuary.

environments if presettlement forms are abundant on flood tides. Other particles have been found to accumulate in fronts at this stage of the tide. Dustan and Pinckney (1989) found that aggregations of phytoplankton were found in fronts only on flood tide in Charleston Harbor (USA).

The nature of general circulation patterns with depth, and circulations related to the pycnocline and front are all favourable for the retention of planktonic organisms in the vicinity of plumes. As the behavioural repertoire of larvae increases, a combination of vertical and horizontal movements in response to the physical and biological attributes of the plume would greatly increase their chances of being retained in the area. Sinclair (1988) argued that the size and number of retention areas determine the number and size of fish stocks. Although retention near a suitable settlement site or within the geographic boundaries of a stock is a plausible hypothesis, it is also possible that the retention and production of suitable food is influencing survivorship to recruitment (Therriault and Levasseur 1986; Lohrenz *et al.* 1990; Fortier *et al.* 1992; and see *Feeding Growth and Mortality* below). The relative importance of these mechanisms may vary with the size of plume. For example, retention may be more important in small plumes where nutrient input and potential trophic impact is low.

It is important to view the dynamics of plume size and directions of water movement in relation to other coastal

processes. For example, some small plumes appear to dissipate on the flood tide (e.g. Kingsford and Suthers 1994). It is possible that ichthyoplankton could be carried alongshore if local ocean currents are stronger than tidal currents moving toward the plume. Ocean currents and wind (e.g. Epifanio *et al.* 1989) can have a strong influence on the nature of currents in plume regions, and these physical attributes would have to be factored into physical models that describe and predict variation in the size of plumes as retention areas and direction of transport.

The spawning behaviour of adults may facilitate the concentration and retention of larvae in fronts and plumes. Bluefish, *Pomatomus saltatrix*, (Sabatés and Martin 1993), butterfish, *Perprilus burti*, (Herron *et al.* 1989), exocoetids (B. Lavenberg, personal communication), and probably other species as well, aggregate and spawn in the vicinity of plumes and fronts. Presumably this behaviour is adaptive and results in increased survivorship.

Feeding, Growth and Mortality

Ecological conditions in riverine plumes in general, and at their fronts in particular, may be favourable for fish larvae. As previously pointed out, light and nutrient conditions support high primary production and accumulation of phytoplankton biomass. These conditions, found relatively infrequently in the sea, occur at

Table 5. Diet and nutritional condition of fish larvae associated with various river discharge plumes
Size: L, large; S, small (see Table 1). Method: D, Diet; M, Morphological; B, Biochemical

River	Size	Species	Method	Trophic Advantage	Reference
Mississippi	L	<i>Anchoa hepsetus</i>	D	yes	McNeil and Grimes 1994
		<i>Leiostomus xanthurus</i>	D	no	Govoni and Chester 1990
		<i>L. xanthurus</i>	D,M	no	Powell <i>et al.</i> 1990
		<i>A. hepsetus</i>	B	yes	Torres <i>et al.</i> unpublished
Botany Bay	S	<i>Kyphosis</i> sp.	D	no	Rissik and Suthers in press
		<i>Liza argentea</i>	D	no	
		Mullidae	D	yes	
Tokyo Bay	S	Blennidae	D	yes	Iwatsuki <i>et al.</i> 1989
		<i>Hexagrammos</i> spp.	D	no	
Gulf of St Laurence	S	<i>Mallotus villosus</i>	D	yes	Fortier <i>et al.</i> 1992
		<i>Ammodytes</i> sp.	D	yes	
		<i>Sebastes</i> sp.		no	
		<i>Stichaeus punctatus</i>	D	no	

hydrographic singularities such as riverine plume fronts and support the short food chain in which large phytoplankton cells are grazed directly by copepods (Cushing 1989; Legendre and Le Fevre 1989). The observation of these conditions at fronts led Holligan (1981) and Holligan *et al.* (1983) to offer the high-productivity theory (Le Fevre 1986) that enhanced phytoplankton production in frontal regions should be reflected in zooplankton abundance and be of importance for fish and fishing activities. It has been more explicitly hypothesized that fish larvae at the Mississippi River plume front may experience enhanced feeding conditions (Govoni *et al.* 1989; Finucane *et al.* 1990; Grimes and Finucane 1991), grow faster and thus experience a briefer larval stage and survive better (Grimes and Finucane 1991). However, the same physical and biological dynamics that lead to accumulated larval fish prey may also accumulate their predators (Govoni *et al.* 1989; Grimes and Finucane 1991), so that any advantage of better diet resulting in faster growth must be weighed against possible higher mortality from predation (Grimes and Finucane 1991).

The several elements of this hypothesis have been evaluated only to a limited degree. For example, it can not be stated unequivocally that fish larvae associated with plumes in general, or with their fronts in particular, are conferred a trophic advantage, or how any trophic advantage might vary with the scale of the river plume (Table 5). Spot, *Leiostomus xanthurus*, larvae collected off the large Mississippi River plume ate twice as many food organisms as did larvae in Gulf of Mexico shelf waters (Govoni and Chester 1990). However, organisms within the plume were mostly small (tintinnids, copepod nauplii, pelecypod veligers and invertebrate eggs), whereas organisms eaten in shelf waters were larger (copepodids and adult copepods). Because the

volume and nutritional quality of gut contents of larvae from the two areas were roughly equivalent, it was concluded that larvae in the plume gained no trophic advantage. Similarly, Powell *et al.* (1990) used morphological, gut-content and recent growth criteria to evaluate nutritional condition of spot larvae associated with the Mississippi plume and could not consistently demonstrate an advantage. A diet study on striped anchovy, *Anchoa hepsetus*, collected along transects crossing plume, front and shelf waters off the Mississippi plume indicated that diatoms and copepods were by far the dominant food items, and that the larger more nutritious copepods occurred more frequently and accounted for the highest percentage of food items in guts of larvae collected in frontal waters, followed by plume then shelf waters (McNeil and Grimes 1995). A suite of biochemical indices to nutritional condition (RNA/DNA ratio, amount of protein [%] and citrate synthase and lactate dehydrogenase enzyme systems), were examined in striped anchovy collected along the same transects off the Mississippi plume; larvae collected in frontal waters were in the highest nutritional condition (J. Torres *et al.*, unpublished). Rissik and Suthers (1996) examined trends in gut fullness in three taxa of fish larvae in plume, front and ocean waters of Botany Bay, Australia. They could not demonstrate that *Kyphosis* sp. and *Liza argentea* gained a trophic advantage, whereas Mullidae larvae did. Furthermore, they cautioned that these findings were inconclusive because the scale of sampling (plume, front and ocean samples separated by 200 m) and the dynamic nature of the front with respect to position and intensity of convergence made it likely that fish that were collected in plume, front or ocean waters may have been in another water mass a few hours earlier.

As previously mentioned, some taxa appear to be associated with plumes and their fronts, and they may be

better adapted than others to take advantage of abundant food resources in plume fronts. Off Tokyo Bay, Japan, Iwatsuki *et al.* (1989) found that blennioid larvae ate over twice as many adult copepods and over three times more nauplii in frontal waters than in shelf waters. However, they did not observe a similar pattern for *Hexagrammos* spp. larvae. In the small-scale buoyancy-driven coastal jet of the St Lawrence estuary off the Gaspé Peninsula, Canada, Fortier *et al.* (1992) reported that the small abundant larvae of capelin, *Mallotus villosus*, and sand lance, *Ammodytes* sp., were associated with the intense production of their food in the frontal conditions of the coastal jet, but that large less-abundant redbfish, *Sebastes* sp., and Arctic shanny, *Stichaeus punctatus*, were not. Thus, it may be that small abundant opportunistic species like anchovies, capelin, sand lance and blennies are well adapted to take advantage of high food concentrations at oceanographic singularities like riverine plumes and their associated fronts. Large, less abundant and more competent larvae of species such as *Sebastes* sp., *Hexagrammos* spp. and *S. punctatus* are not, but may be more fit to colonize less productive areas of the sea (Fortier *et al.* 1992). Furthermore, it is likely that, irrespective of the scale of river plume, where the physical and nutrient dynamics allow high primary and secondary production and formation of the short food chain, appropriately adapted species of fish larvae may be able to gain a trophic advantage.

A second element of the high-productivity hypothesis applied to river plumes states that fish larvae that are conferred a trophic advantage at riverine plumes and their associated fronts will respond by growing faster, and there is some evidence that growth of some fish larvae, as determined from otolith microstructure, may be enhanced. Growth of king mackerel, *Scomberomorus cavalla* was higher off the Mississippi River plume (0.95 mm day^{-1}) than at other localities in the Gulf of Mexico (0.79 mm day^{-1}) (DeVries *et al.* 1990). However, superior growth off the plume was not demonstrated for Spanish mackerel, *Scomberomorus maculatus* (DeVries *et al.* 1990), or little tunny, *Euthynnus alletteratus*, (Allman and Grimes, in press). Other results for Spanish mackerel (Grimes and DeVries, unpublished; and Fig. 6) as well as those for yellowfin tuna, *Thunnus albacares*, (Lang *et al.* 1994) and striped anchovy, *Anchoa hepsetus*, (Day 1993) suggest that larvae associated with the Mississippi plume grow faster at intermediate salinities, i.e. frontal waters (0.6 v. 0.75 mm day^{-1} and 0.5 v. 0.67 mm day^{-1} , respectively, for yellowfin tuna and striped anchovy). Although we are not aware of similar studies on small riverine plumes, it seems reasonable to conclude that, regardless of the magnitude of river discharge, if physical and nutrient dynamics allow high food production for fish larvae, some species (at least opportunistic ones) will respond with increased growth.

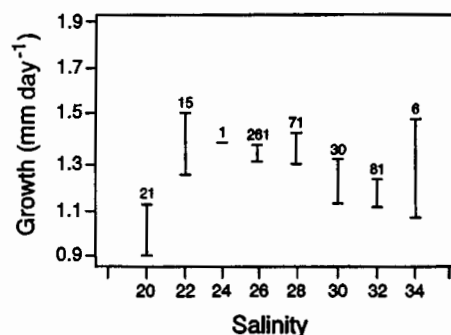


Fig. 6. Average growth (length/age) per day and sample size for Spanish mackerel larvae collected in the vicinity of the Mississippi River discharge plume on salinity. Error bars represent 95% confidence intervals. Intermediate salinities represent the frontal region.

The final element of the high-productivity hypothesis as applied to riverine plumes states that faster growth leads to shorter duration of the larval stage and better survival, with the caveat that the same dynamics that concentrate prey of fish larvae might also concentrate their predators. There is little evidence to evaluate this element of the hypothesis, or to consider what the effects of the scale of discharge might be on survival/mortality dynamics. Grimes and DeVries (unpublished) estimated instantaneous rates of natural mortality for Spanish mackerel and king mackerel in the vicinity of the Mississippi River discharge in the Gulf of Mexico using a catch-curve approach (i.e. regressing the \log_e of frequency on age of the descending limb of age-frequency histograms). Instantaneous natural mortality estimates were approximately 0.3 day^{-1} away from the plume and 0.6 day^{-1} or higher in the vicinity of the plume. For little tunny, instantaneous natural mortality was slightly higher in the vicinity of the Mississippi River plume (0.94 day^{-1}) than in the Gulf of Mexico off Panama City, Florida (0.85 day^{-1}) (Allman and Grimes, in press). Similar analyses for striped anchovy in water masses off the Mississippi River suggest that natural mortality in the front (0.13 day^{-1}) and plume (0.23 day^{-1}) may be higher than that experienced in shelf waters (0.09 day^{-1}) (Day 1993). Conversely, yellowfin tuna (Lang *et al.* 1994) experience higher natural mortality at fronts (0.41 day^{-1}) than in the plume area in general (0.16 day^{-1}). These differences in mortality rates should be interpreted with caution. Application of catch-curve or survivorship analysis to estimate instantaneous mortality rates assumes equal vulnerability to capture by the sampling gear for all ages used in the analysis. Faster growth rates might lead to biased mortality estimates because fast-growing larger larvae become less vulnerable to capture and would be under-represented at the older ages used in the analysis. Although these results are tentative they do not support the contention that higher growth rates of larvae associated with river

plumes lead to better survival. As with the previous elements of the high-productivity hypothesis applied to fish larvae, there is no obvious reason why these dynamics of larval fish mortality would vary with scale of the river plume for plumes that are large and persistent enough to display the physical and biological dynamics herein described.

Recruitment

It seems clear that discharge plumes of major rivers like the Amazon, Zaïre (Congo) and Mississippi can play a significant role in the recruitment of local fishes; the exact mechanisms through which this occurs are less clear. As pointed out, such rivers drain large land masses (e.g. the Mississippi River drainage basin includes over 40% of the contiguous United States) and discharge large volumes of nutrients and suspended materials producing shallow turbid plumes that can extend more than 100 km into coastal waters (Table 1). The physical dynamics and nutrient conditions in the vicinity of discharge plumes often generate large stocks of phytoplankton, zooplankton and ichthyoplankton, and high rates of primary and secondary production. Physical dynamics not only act to accumulate (and probably retain) biomass in frontal waters under certain conditions, but also transport planktonic organisms onshore, offshore and along the frontal boundary. Furthermore, some fish spawn in association with plumes (e.g. pomatomids and clupeids), and stocks of fish larvae off river plumes are often much larger than in adjacent ocean areas.

Major fisheries have been eliminated or have declined when river flows were controlled. For example, totoaba, *Totoaba macdonaldi*, the largest sciaenid in the world (to 2 m and 100 kg), once supported important commercial and recreational fisheries in the northern Gulf of California. In 1976, the totoaba was placed on the endangered species list, its decline due at least in part to the diversion of the Colorado River drastically altering the spawning and nursery area in the vicinity of the delta (Barrera-Guevara 1990). Similarly, filling of the Aswan Dam began on the Nile River in 1965 and was completed in 1969, during which time the flow decreased by $40 \text{ km}^3 \text{ year}^{-1}$, with a concomitant decline in primary production off the delta. Egyptian fishery catches in the Mediterranean Sea declined from 37800 t in 1962 to 7142 t in 1976, with an attendant simplification of fish community structure (Bebars and Lasserre 1983). Declines in these fisheries included the valuable prawn fisheries (Bishara 1984), and the sciaenid *Argyrosomus regius* whose major reproduction and nursery areas were off the Nile delta (Quero 1989).

In considering the potential effects of scale of the river discharge on recruitment we present three alternative hypotheses describing the possible mechanisms through which riverine discharge impacts recruitment. The short-

food-chain hypothesis states that recruitment will be enhanced in the vicinity of river plumes because fish larvae there experience superior feeding conditions, grow faster and thus have a briefer larval stage and survive better (Grimes and Finucane 1991). It appears that some species of fish larvae (opportunistic ones) are able to take advantage of abundant prey resources. Also, some species of fish larvae appear to grow faster, but mortality rates may also be higher. So, whether this hypothesis is valid, and the population dynamics of fish larvae in the vicinity of river plumes favour recruitment, depends on the relative magnitude of growth and mortality. A simple and convenient way to evaluate the relative importance of growth and mortality is to use the expression of exponential decay in population size with time $N_t = N_0 e^{-zt}$, where N_t is population at time t , N_0 is initial population, and z is instantaneous mortality; z can be directly estimated and $t = L_c/g$ (where L_c is a critical size where mortality decreases markedly and g is growth rate [directly estimated]). The product of zt is an exponent that determines the decrease in N_0 . Obviously, the effect of z on N_0 (survival to the critical size, L_c) is much greater than g , because z is a direct multiplier and g is a fractional multiplier (the divisor of L_c). Thus, incremental changes in mortality will have a much larger effect on survival and recruitment than will incremental changes in growth rate. Hence, if physical and biological conditions in the vicinity of plumes aggregate larval fish prey, leading to a trophic advantage and faster larval growth, but also aggregate predators and increase the mortality rate on larvae, the disadvantage of increased mortality may well outweigh the advantage of faster growth, and increased survival and recruitment will not be the result. However, we emphasize that accurate estimates of larval mortality rate are difficult to obtain by the time-specific approach usually taken, owing mainly to sampling bias associated with gear selectivity and the contagious distribution of fish larvae in time and space. In addition, the actual rates of predation and resulting mortality may vary widely owing to the contagion in the distribution of fish larvae and their predators in time and space, and the match-mismatch of prey and predators.

A second alternative possibly explaining the apparent favourable effect of river plumes on recruitment, the total-larval-production hypothesis, is that trophic conditions support such high total production of fish larvae that negative effects of unfavourable dynamics are overridden. That is, high primary and secondary production associated with plumes may simply support such high total production of fish larvae that the specific population dynamics at plumes are not often relevant. If fish spawn in association with plumes, which this hypothesis implies, they evolved to do so because it was adaptive, i.e. progeny produced in the plume survive better and make a larger contribution to subsequent generations. This is a problem with this

hypothesis, because it is difficult to imagine how this system would have evolved.

A third hypothesis is that plumes and associated circulations facilitate the retention of larvae within an area. The presence of food would of course be important, but variation in physical retention rather than production may explain variation in recruitment, as argued for the member/vagrant hypothesis of Sinclair (1988). It is very difficult to isolate the relative contribution of variable input of nutrients and intensity of the retention mechanism because both vary with riverine input and mixing with coastal currents. It is unlikely that there are plumes where the input of nutrients varies while the physical mechanisms remain the same (or vice versa). If any of these hypotheses are valid, the scale of the discharge plume is very important to the potential impact upon fish recruitment, and generally we expect that the larger the plume the greater its impact will be. The greatest potential for a major impact on fish recruitment is probably found in mid-latitude rivers, such as the Mississippi River, that carry high suspended-sediment and nutrient loads and discharge into shelf waters, thereby creating well defined plumes where primary and secondary production are high.

There are additional factors that could also bear on the importance of a given river plume to recruitment. It is probably important that receiving shelf waters are not adjacent to strong ocean currents that would reduce larval retention and quickly dilute and dissipate nutrient concentrations and resulting effects on primary and secondary production. Local oceanography could be changed by interactions with ocean currents that might change seasonally or through physical forcing such as the southern oscillation.

It seems intuitive that the greatest impacts on recruitment might be expected in tropical river plumes where receiving ocean waters are oligotrophic and have low-amplitude production cycles. This scenario is not well supported by available data, because production in tropical river plumes is often barely higher than that in adjacent waters. However, it is possible that even small changes in production have important consequences for recruitment of fish.

The ability to detect significant effects of river plumes on variation in levels of recruitment will depend on the magnitude and predictability of the local production cycles and retention mechanisms that are unrelated to the input of fresh water from river plumes. For example, at temperate latitudes there are distinct seasonal peaks in production, generally spring and autumn (Cushing 1975). Additional production that results from freshwater intrusions that occur at the same times may be difficult to identify unequivocally. Therefore, it is important to simultaneously consider the relative importance to recruitment of various coastal processes, including plumes, that may contribute to variation in recruitment.

In conclusion, there is a significant body of evidence that river discharge plumes of different sizes and latitudes influence fish recruitment. The physical attributes of the plume and frontal regions and variation in primary and secondary production are potentially responsible for this variation. One or a combination of hypotheses may explain this variation: (1) the short-food-chain hypothesis, where variation in feeding conditions leading to variation in growth and mortality explains variation in recruitment; (2) the total-larval-production hypothesis, where a combination of intense spawning by adults and retention of larvae results in high numbers of fish larvae and the importance of the plume area is maintained even when mortality is high; and (3) the larval-retention hypothesis, where variation in the size and intensity of the plume-related retention area explains variation in recruitment. Regardless of the processes influencing the dynamics of larval abundance and subsequent recruitment, plumes and associated frontal regions have a major influence on ichthyoplankton, and care should be taken that conditions are not compromised by environmental degradation.

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